HABITAT RELATIONSHIPS OF THE PACIFIC COAST SHRUB *OEMLERIA CERASIFORMIS* (ROSACEAE)

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ABSTRACT

Oemleria cerasiformis is a common shrub in parts of the Pacific Northwest, but little is known about its autecology. To examine the habitat relationships of this species, we sampled 56 stands representing most of its geographical range. These stands contained a diverse array of woody species, indicating considerable variation in the habitats occupied. DCA ordinations for all stands and for various subsets indicated that moisture, disturbance, and phytogeographical patterns are important variables among stands. Both in the Willamette Valley, Oregon, and on southeastern Vancouver Island, B.C. (areas where it is common), *O. cerasiformis* occurs along a moisture gradient from *Quercus garryana* woods through *Pseudotsuga menziesii* forests to streamside groves of *Alnus rubra.* In areas too dry for growth on uplands and in areas of wet coniferous forest, *O. cerasiformis* occurs primarily along streams. It is common on upland sites only in the narrow segment of the regional moisture gradient that spans the transition from *Q. garryana* to *P. menziesii* forests.

Oemleria cerasiformis (Hook. & Arn.) Landon (*Osmaronia cerasiformis* (Torrey & A. Gray) E. Greene), hereafter *Oemleria,* is a large shrub that occurs along the Pacific coast of North America. The monotypic genus *Oemleria* is similar to *Prunus* in many respects, but is dioecious and has multiple pistils per flower. It blooms in February or March over most of its range. Both sexes have racemes of small white flowers. Males and females differ somewhat in flowering phenology (Allen 1986), and the males on average produce more flowers than the females (Allen and Antos 1988). The fruits are drupes (much like those of *Prunus*) and ripen in May or June, and each of the five pistils in a female flower can produce a fruit.

Oemleria leafs out in February to March (sooner than most associated deciduous shrubs), and forms few new leaves after May. The leaves are generally retained until autumn, but on drier sites 50% or more of the leaves can be shed during dry periods in July and August.

Individual plants can grow to 7 m in height, and can form large clumps with ten or more closely spaced stems. The plants do not spread via rhizomes or root sprouts, but layering of stems may occasionally give rise to new clumps. Layering is rare, except in old forests where plants are sometimes bent over by falling trees.

Oemleria occurs west of the Cascade Range and the Sierra Nevada from southwestern British Columbia to central California, and is

MADROÑO, Vol. 37, No. 4, pp. 249–260, 1990

most common from central Oregon northward. To the south it becomes more restricted to wet habitats. Populations generally have male-biased sex ratios (Allen and Antos 1988), but we have found no niche differences between sexes (Allen and Antos unpubl.).

Little information is available on the habitat requirements of *Oemleria.* In conjunction with a study of sex ratios (Allen and Antos, unpublished data), we determined the species composition of stands containing *Oemleria* throughout much of its range. In this paper we present these results, and make inferences from them about the ecological requirements of *Oemleria.*

Methods

We examined potential sample sites throughout the range of *Oemleria* (Fig. 1), and sampled wherever it was reasonably abundant. Sampling was concentrated in the Willamette Valley of Oregon and on Vancouver Island, B.C., areas where *Oemleria* is especially common. We chose sites to encompass as much of the variation in habitats of *Oemleria* as possible. Sites were sampled if they (1) contained 100 or more mature individuals (enough to obtain a good estimate of sex ratio) and (2) were fairly homogeneous with respect to topography and vegetation. We relaxed the first criterion occasionally in habitats where it was difficult to find large populations. *Oemleria* often occurs in ecotones (e.g., margins of woods) and in patchy habitat mosaics. Thus the areas sampled were variable in size, and often irregular in shape.

At each site, we first examined *Oemleria* plants to determine the sex ratio and then recorded habitat characteristics for the area circumscribed by these plants. We visually estimated canopy cover for each woody species within the area, as well as total cover of trees, tall shrubs and low shrubs. Herbaceous plants were excluded because we sampled when *Oemleria* was in bloom, prior to the emergence of many herbaceous species. We also made observations on site characteristics, stand structure, and probable past disturbances.

To examine patterns of variation among sites, we produced ordinations using Detrended Correspondence Analysis (Hill and Gauch 1980). We included cover data for all taxa present in more than two sites. All cover values were log transformed. Ordinations were obtained for (1) all sites, (2) sites on Vancouver Island, and (3) sites in the Willamette Valley. To aid in interpretation of ordination axes, we examined species patterns plotted on the ordinations.

Nomenclature follows Hitchcock and Cronquist (1973) or Munz (1973).

Results

All sites. Stands from different geographical regions differed in average composition (Table 1), and were generally separated on the

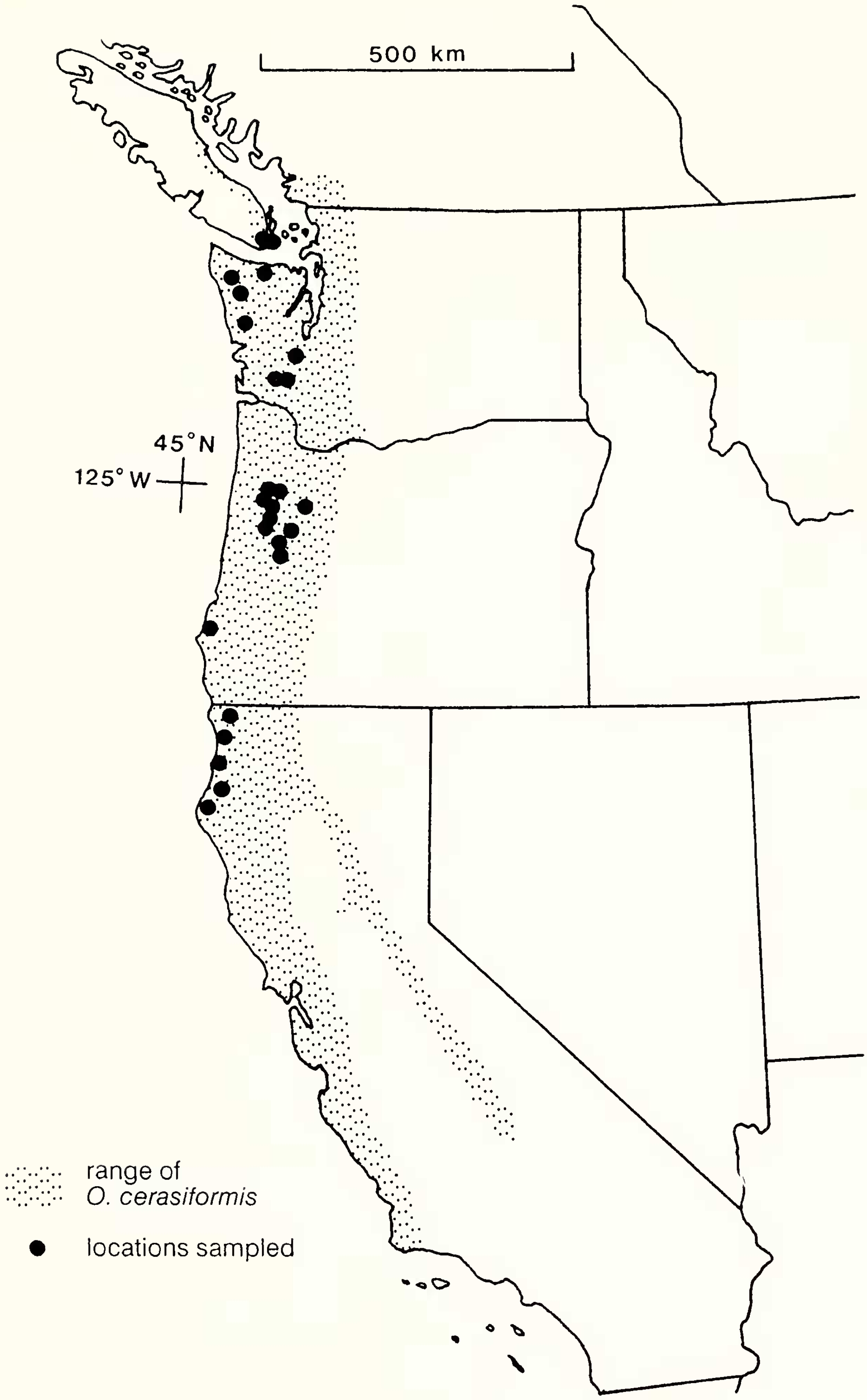

FIG. 1. Map of western North America showing the approximate range of *Oemleria cerasiformis* (stippled area) and locations sampled (black circles). Some circles, especially in the Willamette Valley and on Vancouver Island, represent more than one population sampled in the same general area.

TABLE 1. SPECIES GROWING IN STANDS CONTAINING *OEMLERIA CERASIFORMIS* BY GEOGRAPHICAL REGION. Cover is the mean percentage for all stands in a category; constancy is the percentage of stands in which a species was present. Only species that had at least 1% cover and 50% constancy in one region are included.

	Vancouver Island n = 20		Washington n = 9		Willamette Valley n = 21		California and Southern Oregon n = 6	
	Cover	Con.	Cover	Con.	Cover	Con.	Cover	Con.
Trees								
Abies grandis	7.6	70	2.2	11	1.0	67	2.5	33
Acer macrophyllum	14.8	70	8.6	67	24.4	90	7.5	83
Alnus rubra	10.3	35	38.5	89	10.3	43	31.7	100
Crataegus spp.	1.0	50	0	0	1.7	67	0	0
Fraxinus latifolia	0	0	3.7	11	9.2	76	0	0
Lithocarpus densiflorus	0	0	0	0	0	0	5.0	50
Picea sitchensis	0	0	8.9	67	0	0	10.0	50
Populus trichocarpa	0.6	15	5.3	56	2.7	57	14.2	17
Prunus avium	0.4	25	0	0	1.7	62	0	0
Pseudotsuga menziesii	32.0	65	5.7	56	16.7	86	17.5	67
Quercus garryana	18.8	50	0	0	12.7	71	0	0
Rhamnus purshiana	2.8	75	0.3	22	1.9	76	4.1	67
Salix spp.	1.0	15	1.2	56	0.1	14	12.3	83
Sequoia sempervirens	0	0	0	0	0	0	5.8	50
Thuja plicata	5.2	50	1.4	44	0.4	14	0	0
Tsuga heterophylla	0.1	5	1.6	56	0.1	14	0	0
Umbellularia californica	0	0	0	0	0	0	3.3	50

TABLE 1. Continued.

	Vancouver Island n = 20		Washington n = 9		Willamette Valley n = 21		California and Southern Oregon n = 6	
	Cover	Con.	Cover	Con.	Cover	Con.	Cover	Con.
Shrubs								
Acer circinatum	0	0	11.0	78	15.8	62	0	0
Amelanchier alnifolia	0.8	30	0.1	11	1.5	57	0	0
Berberis nervosa	3.6	55	0.1	11	0.3	10	0.8	17
Corylus cornuta	0.3	10	0.2	11	19.4	95	0.3	17
Gaultheria shallon	2.0	15	2.1	56	0.3	14	0	0
Holodiscus discolor	6.5	65	0.9	11	1.9	76	7.5	33
Ilex aquifolium	1.5	55	0.1	11	0	0	0	0
Philadelphus lewisii	0.7	20	0	0	1.0	57	0	0
Physocarpus capitatus	0.7	20	0.9	11	1.7	57	0	0
Rhus diversiloba	0	0	0	0	5.5	52	1.7	17
Rubus discolor	2.0	60	0.6	11	9.0	81	0	0
Rubus parviflorus	0.1	10	1.7	44	0.9	38	10.8	83
Rubus spectabilis	3.8	20	21.8	89	3.0	29	18.3	50
Rubus ursinus	5.1	80	0.2	11	5.3	86	40.8	100
Sambucus racemosa	0.3	15	6.3	78	0.4	29	25.8	50
Symphoricarpos albus	36.8	100	7.1	67	30.0	100	0	0
Vaccinium ovatum	0	0	0	0	0	0	5.2	50

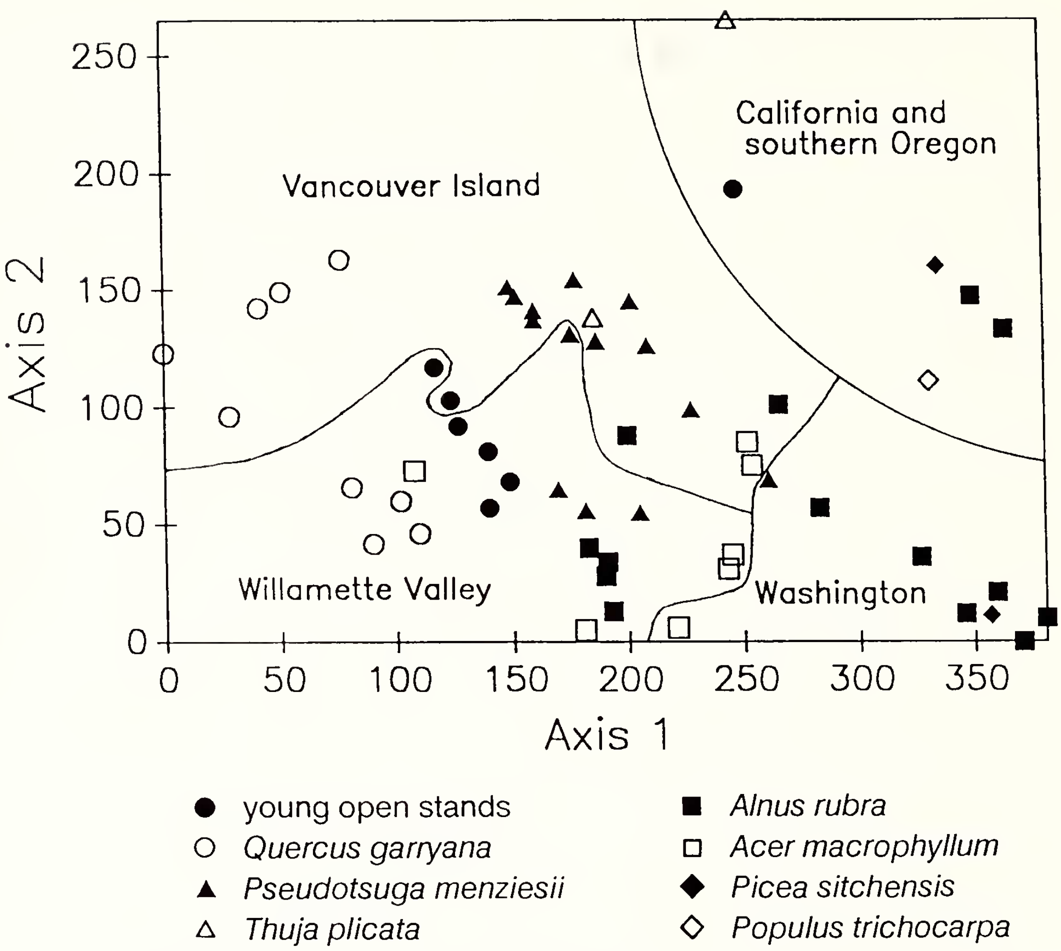

FIG. 2. Ordination (axes 1 and 2) from Detrended Correspondence Analysis for all 56 stands. The lines separate stands from different geographical regions. The symbols indicate the most abundant (highest cover) tree species at the forested sites.

ordination (Fig. 2). Two patterns are apparent: a moisture gradient related to exposure to Pacific storms, and a north-south floristic gradient. Relatively dry *Quercus garryana* stands were on the left side of the first axis, wet *Alnus rubra* stands were on the right side, and *Pseudotsuga menziesii* stands occupied the center (Fig. 2).

Although moisture generally increases to the north in the study area, the stands did not separate out in a simple north-south pattern (Fig. 2). Dry-site species such as *Quercus garryana* and *Symphoricarpos albus* were common in stands from the Willamette Valley and from Vancouver Island (Table 1), which are sheltered by the Oregon Coast Range or the Olympic and Vancouver Island Mountains. In contrast, the wetter-site species, *Picea sitchensis* and *Rubus spectabilis* occurred primarily in the Washington and California stands, which are directly exposed to storms from the Pacific.

The non-forest stands, most of which were in early stages of succession to forest, were located on the ordination primarily between the dry *Quercus* stands and the wetter stands containing conifers, *Acer macrophyllum,* or *Alnus rubra.* The location of non-forest stands toward the drier end of the moisture gradient represented by the first ordination axis is related to the presence of species characteristic of open habitats.

The second ordination axis in Fig. 2 reflected phytogeographical patterns. *Acer circinatum* and *Fraxinus latifolia* occur in the Willamette Valley and Washington stands but are absent from the other stands (Table 1), which may explain why stands from both the north and south ends of the study area occurred at the top of the ordination. The stands sampled span a long north-south gradient, and along this gradient many species reach range limits or change drastically in abundance.

In order to reveal underlying patterns that might be obscured by the strong phytogeographical gradient in the overall data set, we examined different geographic areas separately. For the two areas for which we had concentrations of 20 or more sample stands, we performed separate ordinations.

Vancouver Island. The stands sampled were all on the extreme southeast end of the island, which is the driest part. *Oemleria* is abundant in a variety of habitats in this area, but is uncommon elsewhere on the island. The ordination of the 20 stands from Vancouver Island indicated one major gradient, a moisture gradient from dry *Quercus* stands to wet *Alnus* stands (Fig. 3). The *Quercus* stands clustered on the right side of the ordination; they generally had deep soils, often with a high cover of *Oemleria* and *Symphoricarpos albus.* The driest *Quercus* stands in the area, which occurred on shallow soils over bedrock, supported few or no *Oemleria.* The *Quercus* forests grade into moderately dry coniferous forest dominated by *Pseudotsuga menziesii. Oemleria* is often the most common tall shrub species in these forests. Most forests on Vancouver Island are wetter than those containing *Oemleria* and would extend along the moisture gradient off to the left side of the ordination.

Washington. The stands sampled in Washington generally had *Alnus rubra* as the dominant canopy tree, and shrubs typical of wet sites, especially *Rubus spectabilis,* were common (Table 1). These sites were wet enough to support dense coniferous forest but had undergone human disturbance or were on stream bottoms where the vegetation is naturally disturbed by alluvial activity. *Oemleria* occurs in some very old riparian rainforests on the Olympic Peninsula.

Willamette Valley. In Oregon, *Oemleria* is common in the Willamette Valley and occurs along streams far into the surrounding mountains. It is much less common along the coast, where it occurs on sites similar to those sampled in Washington. Sampling was concentrated in the Willamette Valley and adjacent parts of the Cascade and Coastal Mountains. The first axis of the ordination of Willamette Valley sites represented a moisture gradient from *Quercus garryana* forests on the valley bottom to *Acer macrophyllum–*

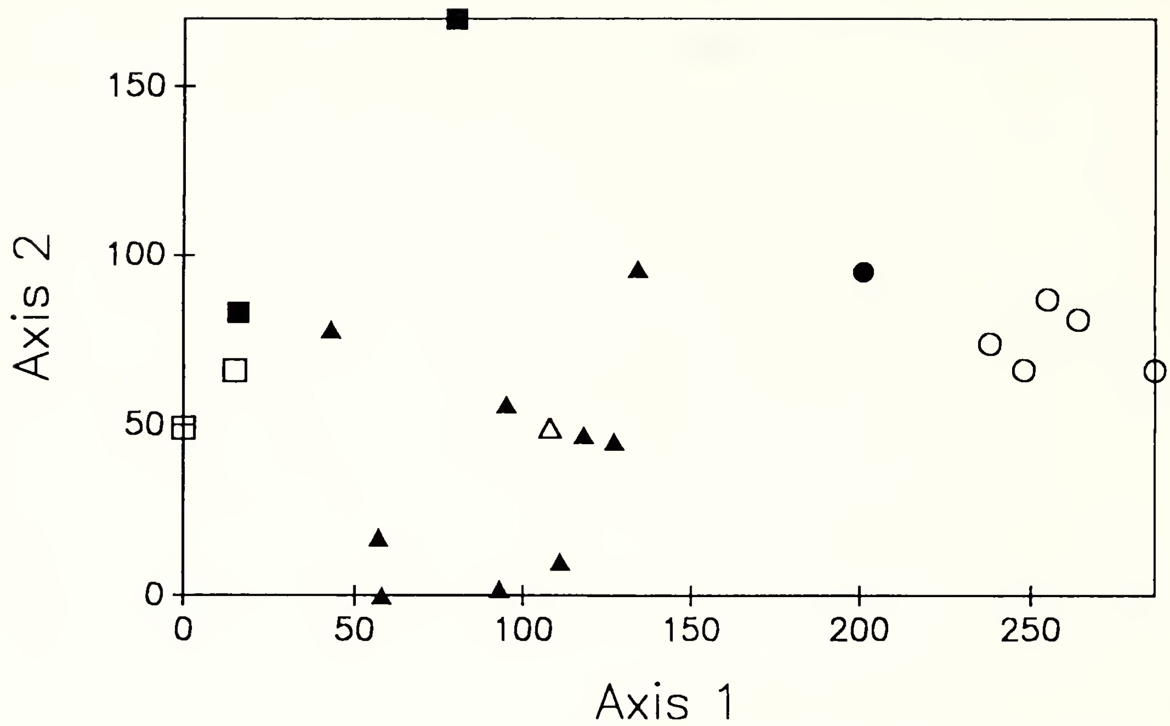

FIG. 3. Ordination (axes 1 and 2) from Detrended Correspondence Analysis of 20 stands on Vancouver Island. Symbols as in Fig. 2.

Alnus rubra forests along mountain streams (Fig. 4). The second axis represented a gradient from streamside *Alnus rubra* forests, often with considerable *Fraxinus latifolia,* to well drained *Pseudotsuga menziesii* forests. The open sites, in the upper left region of the ordination (Fig. 4), were mostly abandoned pastures with scattered old trees and a few young trees and shrubs.

Although *Oemleria* is common in the Willamette Valley, especially along streams, it is virtually absent from many types of sites. It is common in *Quercus garryana* forests on alluvial bottoms, but rare on very wet sites dominated by *Fraxinus latifolia.* It occurs in some upland *Quercus* and *Pseudotsuga* forests adjacent to the Willamette Valley. However, it is found primarily in wetter microsites within these forests, so many of these forests may be too dry to support *Oemleria.* Farther into the mountains, *Oemleria* is generally confined to relatively open streamside forests.

Southern sites. The six southernmost stands sampled did not clump tightly on the ordination of all sites (Fig. 2), and they varied considerably in composition. They were all near the coast (one in southern Oregon and five in California) and were fairly wet, as indicated by the high cover and consistent occurrence of *Alnus rubra* (Table 1). Other species present, such as *Picea sitchensis, Sequoia sempervirens,* and *Rubus spectabilis,* also indicate wet sites. Most of these stands had been affected in the past by human disturbances (primarily logging). In the *Sequoia* zone, *Oemleria* can be locally com-

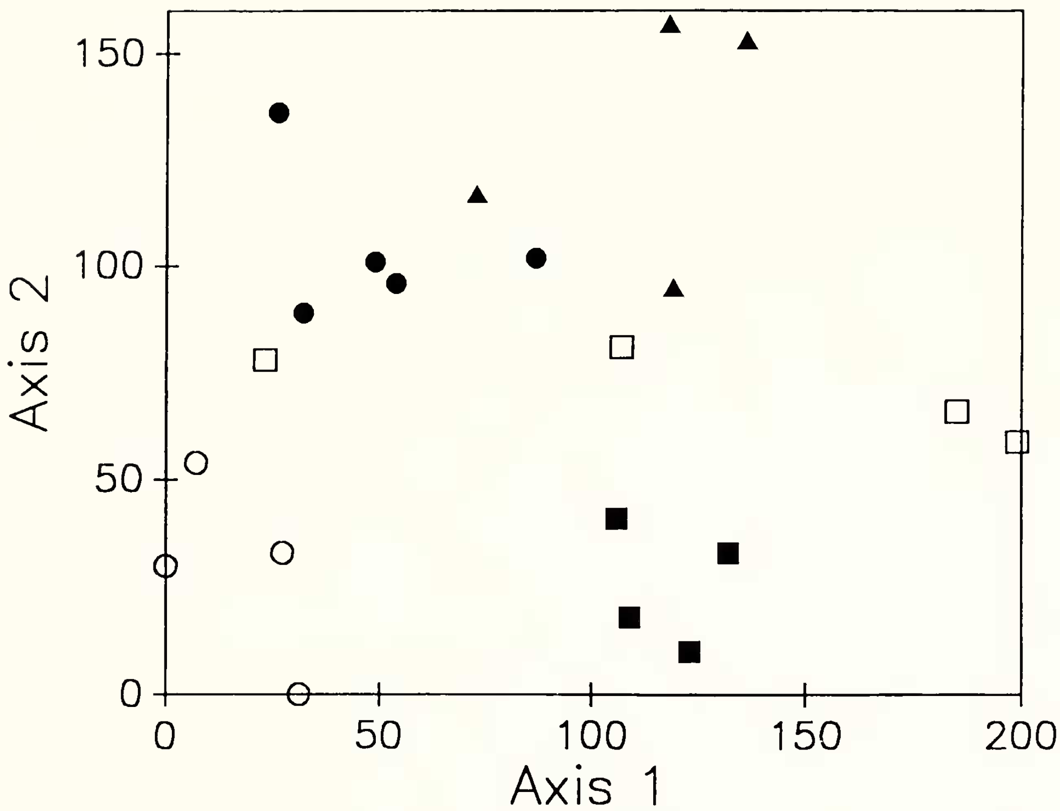

FIG. 4. Ordination (axes 1 and 2) from Detrended Correspondence Analysis of 21 stands in the Willamette Valley. Symbols as in Fig. 2.

mon along streams where the tree canopy remains open, but it is generally absent in upland forests.

Oemleria also occurs inland from the coastal *Sequoia* zone and south to approximately Santa Barbara, but it is rare and no sites were sampled. It occurs in the Sierra Nevada south to Tulare County. In the South Coast Ranges we have observed it in alluvial *Sequoia* forests near the coast and in mixed evergreen hardwood forests along streams farther inland.

DISCUSSION

Oemleria occurs along the Pacific Coast over a distance of 1700 km, but does not extend east of the Cascade Range or the Sierra Nevada. It is most common at low elevations; all stands sampled were below 250 m elevation. *Oemleria* is usually found at low elevations in the northern parts of its range, but can occur at elevations up to 1500 m in California. Thus the plants are generally found in a fairly mild maritime climate.

Although *Oemleria* was the most abundant shrub in some of the forests stands that we sampled, it is uncommon over much of its geographical range and is often restricted to specific types of habitats. In the south, *Oemleria* is rare primarily because most of the landscape is too dry to support it, and it occurs along streams or in other moist locations. Even as far north as Vancouver Island there are sites too dry for *Oemleria,* as indicated by abrupt edges of populations along rocky areas with stunted *Quercus garryana.* We have observed dieback and mortality of *O. cerasiformis* on some *Quercus* sites in British Columbia during dry years. In most of western Washington and coastal Oregon, *Oemleria* occurs along streams in a matrix of wet coniferous forests. It is generally absent from upland sites wet enough to support *Tsuga heterophylla* forest. Thus the abundance of *Oemleria* is greatly limited in the northern part of its range, where wet coniferous forests cover much of the landscape. Its occurrence along streams is probably related to chronic disturbance resulting from alluvial activity. Throughout much of its range, *Oemleria* extends along streams into both wetter and drier areas than it normally occupies in upland vegetation.

Lack of moisture is unlikely to be the reason for the absence of *Oemleria* from wet, upland coniferous forests. The plants are probably unable to survive in the low light environment under dense coniferous canopies. Although *Oemleria* is moderately shade tolerant and grows well under *Quercus garryana* and in open stands of *Pseudotsuga menziesii,* we frequently observed plants dying back (apparently from lack of light) when overtopped by *Abies grandis* or *Thuja plicata.* It is also possible that the soils of wet, upland coniferous forests are unfavorable for *Oemleria,* which normally grows on relatively rich alluvial soils or on soils that developed under hardwood forests or savanna. Many of the *Pseudotsuga* forests in which *Oemleria* grows have developed from *Quercus* woodlands in historic times, as a result of fire suppression.

Oemleria reaches its greatest regional abundance in areas where it grows on upland sites spanning the transition from *Quercus garryana* to *Pseudotsuga menziesii* forests. The abundance of *Oemleria* in the Willamette Valley of Oregon reflects the large areas of such habitat. These areas previously supported fire-maintained *Quercus* savanna or woodland, which has now become *Quercus* or *Pseudotsuga* forest (Franklin and Dyrness 1973; Thilenius 1968). *Oemleria* occurs in *Pseudotsuga* forests that have developed on former prairie sites in Washington (Franklin and Dyrness 1973). In northern California, *Oemleria* sometimes grows with *Quercus garryana* above the fog belt in woodlands that are more similar to those in the Willamette Valley than to other *Quercus* woodlands in California (Sugihara et al. 1987).

Young *Oemleria* plants are most frequent in partially disturbed areas, e.g., under scattered trees in abandoned pastures or along forest margins. First year seedlings can be abundant in forests but seem to rarely survive long except in openings. Even-aged populations are uncommon, and *Oemleria* does not appear to invade open sites rapidly. Young plants usually occur beneath old plants. Seedlings can establish in open grassy areas, but they usually do so in very low density.

Oemleria can be very long-lived. The plants frequently die back when conditions are adverse but often resprout from the base, which may allow them to persist longer under low light conditions, as observed for *Prunus serotina* (Auclair and Cottam 1971). In relatively open forests along streams, *Oemleria* populations can persist because of the occasional establishment of new plants on disturbed microsites and the low mortality rates of shrubs that may pass through multiple generations of stems.

Historically, individual *Oemleria* plants probably were adversely affected by frequent fires because of their thin bark and large size. Fire suppression, which initially may have led to density increases in *Oemleria* populations, also results in succession to coniferous forests, which has probably eliminated populations on some sites. *Pseudotsuga menziesii* can form fairly dense stands on sites too dry for *Oemleria.* If the same processes restricting *Oemleria* in wet coniferous forests also operate in the drier coniferous forests that can develop from *Quercus* woodlands, the species may decrease in abundance on upland sites. Factors that prevent the development of dense coniferous forests, including fires in the past and some forms of human disturbance at present, are important in maintaining the abundance of *Oemleria* on uplands.

In summary, it appears that the local abundance and overall geographical distribution of *Oemleria* are related to: (1) a restriction to a fairly mild, maritime climate, (2) a moisture requirement that restricts its distribution to moist areas over much of its range, (3) an inability to tolerate either low light levels or soil conditions in wet, upland coniferous forests, which greatly restricts its distribution and abundance in the northern part of its range, and (4) a need for some disturbance of the vegetation to allow seedling establishment. Thus, *O. cerasiformis* occurs along streams over a large geographic area, but occurs on upland sites only on a narrow segment of the regional moisture gradient.

Acknowledgments

We thank Jennifer Allen and Terri Suttill for help with field work, and the curators of UC, JEPS, CAS, DAV, OSC, WTU, and V for access to specimens. This work was funded by the Natural Sciences and Engineering Research Council of Canada.

Literature Cited

Allen, G. A. 1986. Flowering pattern and fruit production in the dioecious shrub *Oemleria cerasiformis* (Rosaceae). Canad. J. Bot. 64:1216–1220.

——— and J. A. Antos. 1988. Relative reproductive effort in males and females of the dioecious shrub *Oemleria cerasiformis.* Oecologia 76:111–118.

Auclair, A. N. and G. Cottam. 1971. Dynamics of black cherry (*Prunus serotina* Erhr.) in southern Wisconsin. Ecol. Monogr. 41:153–177.

Franklin, J. F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. Forest Serv. Gen. Tech. Rept. PNW-8.

Hill, M. O. and H. G. Gauch, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47--58.

Hitchcock, C. L. and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. Washington Press, Seattle.

Munz, P. A. 1973. A California flora with supplement. Univ. California Press, Berkeley.

Sugihara, N. G., L. J. Reed, and J. M. Lenihan. 1987. Vegetation of the bald hills oak woodlands, Redwood National Park, California. Madroño 34:192–208.

Thilenius, J. F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. Ecology 49:1124–1133.

(Received 2 Jan 1990; revision accepted 6 Aug 1990.)

ANNOUNCEMENTS

New Publications

Alcock, John. *Sonoran desert summer.* University of Arizona Press, 1615 E. Speedway, Tucson, Arizona 85719, 1990, x, [i], 187, [1] pp., illus., ISBN 0-8165-1150-0 (hardbound), price unknown. [A series of 37 bot. and esp. zool. vignettes for May through Sep.]

Evens, Jules G. *The natural history of the Point Reyes Peninsula.* National Seashore Association, Point Reyes, California 94956, 1988, xiii, 226 pp., illus. (B&W exc. color cover), ISBN 0-911235-02-7 (paperbound), $14.95. [With 7 chapters on climate, geology, flora, fauna, incl. 5 species lists, of this famous area in Marin Co., California. For review see G. M. Fellers, *Wildflower* 2(2): 28–29.]

Murray, David F. and Robert Lipkin. *Candidate threatened and endangered plants of Alaska, with comments on other rare plants.* University of Alaska Museum, Fairbanks, Alaska, 1987, 75, [1] pp., illus., ISBN 0-931163-03-X (spiral bound), price unknown. [On 17 threatened, endangered, and 18 rare spp.]

Wagner, Warren L., Derral R. Herbst and S. H. Sohmer. *Manual of the flowering plants of Hawai'i.* 2 vols. University of Hawaii Press, 2840 Kolowau St., Honolulu, Hawaii 96822, winter 1990, xviii, vi, 1853, [1] pp., 1 pl. (color fp.), B&W text illus., endpaper maps, ISBN 0-8248-1152-6 (hardbound), $85.00. [Contents: *vol. 1:* intro.; methods and scope; geol.; climate; veg.; important collections; abbr.; tax. treatment (phyletic list fam. in Hawaii, keys to higher order taxa; Acanth. to Nyctagin.); *vol. 2:* tax. treatment (Ochn. to Zygophyll., monocotyledons); glossary; biblio.; addendum on *Melicope* (Rut.); illus. vouchers; index.]